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An impact assessment of alien invasive plants in South Africa generally dispersed by native avian species

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Abstract

Invasive alien plant species have been identified as a major threat to biodiversity and the relationship with native avian dispersers may increase their invasion potential. The impact of invasive plant species needs to be quantified using comparable assessment tools across different habitats and species to allocate limited resources to high-priority species. Here, we used the Generic Impact Scoring System (GISS) to assess the impacts of 16 fleshy-fruited alien invasive plant species in South Africa generally dispersed by native avian species. The results showed that fleshy-fruited invasive species have both environmental and socio-economic impacts. The cumulated impact scores for lantana (*Lantana camara*) and the tree of heaven (*Ailanthus altissima*) were the highest, with scores of 42 and 32, respectively. Some species, such as white mulberry (*Morus alba*), camphor tree (*Cinnamomum camphora*), American bramble (*Rubus cuneifolius*) and Brazilian pepper tree (*Schinus terebinthifolius*), had low overall impact scores of 8, 18, 14 and 16, respectively, but scored the maximum impact of 5 for certain mechanisms. Environmental impacts of fleshy-fruited invasive plant species had a high impact magnitude through effects on the ecosystem and vegetation. Socio-economic impacts were mainly through effects on forest production, agriculture and human health. Species with large crop sizes, small seeds and fruit sizes had higher environmental and socio-economic impact magnitude. The information generated in this study is important for guiding resource allocation and preventing the uncontrolled introduction of invasive species in South Africa. The impact of the fleshy-fruited invasive species transcended sectors and, therefore, effective management of invasive species will require the collaboration of multiple and inter-sectoral stakeholders in South Africa.

Keywords
environmental impacts, GISS, impact score, management strategy, NEMBA, socio-economic impacts

Introduction

Invasive alien plants have been identified as a major threat to biodiversity (Gosper and Vivian-Smith 2009; Liu et al. 2017). Depending on the species, invasive alien plants generally reduce species richness (Gaertner et al. 2009), disrupt pollination and dispersal networks (Pyšek et al. 2012), change ecosystem functioning (Andersen et al. 2004; Charles and Dukes 2008), cause economic losses (Novoa et al. 2016; Zengeya et al. 2017) and impact human well-being (Vilà et al. 2011). Invasive alien plant species are introduced either accidentally or intentionally for forestry, agriculture, horticulture (Arriaga et al. 2004), recreation (van Wilgen et al. 2008), restoration (Kumschick et al. 2012) and as ornamentals (Hulme et al. 2018). New introductions or movements of invasive alien plant species within a country are promoted by increased domestic and global travel and trade, making their management a challenge in many countries (Leung et al. 2012; Seebens 2019). Once introduced, invasive alien plants that attract and rely on generalist frugivores for seed dispersal thrive because animal-plant interactions allow for fast recruitment (Jordaan et al. 2011a, b, 2012; Molefe et al. 2020; Traveset and Richardson 2020). The spread of invasive alien plants is further exacerbated by global climate change (Ahmad et al. 2019a, b; Mofu et al. 2019). For frugivore dispersed plant species in South Africa, altered habitats trigger and sustain invasions (Bitani et al. 2020).

Like other parts of the world, South Africa is severely affected by alien plant invasion (Nel et al. 2004; McLean et al. 2018). Alien plant species are the country's most widespread and damaging group of invasives and have been reported to cover approximately 7% of the country (van Wilgen 2018). Amongst invasive alien plants, those with fleshy fruits have high-risk invasiveness (Jordaan et al. 2011b). Species traits have been shown to influence invasiveness (the likelihood of a species being introduced and spreading). Generalist birds have been identified as the most important seed dispersers of fleshy-fruited invasive shrubs and trees (Richardson and Rejmanek 2011). In new habitats, fleshy-fruited invasive alien plants overcome barriers of spread through seed dispersal mutualisms (Aslan and Rejmanek 2011; Jordaan et al. 2011a, b). Bird-plant interactions are equally important to avian dispersers as they gain a nutritious supplementary fruit source (Thabethe et al. 2015; Blendinger et al. 2016). The invasion process and success of avian-dispersed invasive alien plants are influenced by plant morphological (Gosper and Vivian-Smith 2009), chemical (Jordaan and Downs 2012; Blendinger et al. 2016) and phenological traits (Marciniak et al. 2020; Nogueira et al. 2020). Certain traits favour bird-fruit interaction and allow plants to integrate into native seed-dispersal networks (Rojas et al. 2019; Marciniak et al. 2020). For example, plants that produce large fruit crop sizes have a high potential to be consumed by birds (Blendinger and Villegas 2011).

Impacts associated with invasives vary across habitats and taxa (Hawkins et al. 2015; Bacher et al. 2018), but are mainly related to changes to natural environments, society and economy (Jeschke et al. 2014; Measey et al. 2016; Kumschick et al. 2017). Consequently, impacts associated with biological invasions have led to the development of impact assessment tools intending to quantify the impacts posed by alien invasive species (Nentwig et al. 2016; Rumlerová et al. 2016; Bartz and Kowarik 2019). The impact assessment tools are based on scientific evidence (Kumschick et al. 2015; Moshobane et al. 2019), comparable across different regions and taxa (Nentwig et al. 2016) and allow for the synthesis of impact data (Vilà et al. 2019). Several tools have been developed. The two widely used ones are the Environmental Impact Classification for Alien Taxa (EICAT), developed by Blackburn et al. (2014) to quantify environmental impacts and the Generic Impact Scoring System (GISS), developed to assess environmental and economic impacts (Turbé et al. 2017). The GISS has been used for various taxa, including birds (Turbé et al. 2017; Shivambu et al. 2020), mammals (Hagen and Kumschick 2018), amphibians (Measey et al. 2016), fish (Orfinger and Goodding 2018), arthropods (Laverty et al. 2015) and selected plants (Novoa et al. 2016; Yazlik et al. 2018). Using impact quantifying approaches like the GISS gives insights into which species are detrimental so that management prioritises those species with major impacts (Rumlerová et al. 2016) and provides information for decisions relating to the introduction of species (Bartz and Kowarik 2019).

As part of the global biodiversity goals, most countries worldwide are committed to preventing the introduction of high-priority species or minimising their impacts (Moshobane et al. 2019; Verbrugge et al. 2019). The Department of Environmental Affairs (DEA, now Department of Environment, Forestry & Fisheries, DEFF), through the South African National Biodiversity Institute (SANBI), aims to eventually conduct an impact assessment for all listed species as invasive under the National Environmental Management Biodiversity Act (NEMBA). Of the 379 listed terrestrial invasive plant species, only 75 plant species have been assessed (DEA 2016). Assessing the impacts posed by listed species is important to ensure that the listing can be challenged (SANBI 2017). In response to policy-makers' information needs, we aimed to assess the ecological and socio-economic impacts posed by selected fleshy-fruited invasive plant species dispersed by native avian species in South Africa. Additionally, we explored how morphological traits of fleshy-fruited invasive plants relate to their impacts. The results from the present study will assist in providing information for decision-making, allocating resources to control alien invasive plant species and identifying less-studied plants and impacts. In addition, where the study species have not yet been introduced, it will help guide decisions around permitting or prohibiting activities.

Methods

Species selection and literature search

Sixteen fleshy-fruited alien trees or shrubs dispersed by native avian species that occur in the coastal forests of KwaZulu-Natal, South Africa, were selected for this study. The selected plants are listed as invasive under the South African NEMBA. A literature survey, based on published scientific literature and e-literature from Google Scholar (https://scholar.google.com) and Web of Science – ISI Web of Knowledge (hhttps://apps.webofknowledge.com) and the global invasive species database, such as the Global Invasive Species Database (GISD: www.iucngisd.org/gisd) and the Invasive Species Specialist Group (ISSG: www.iucngisd.org/gisd), was conducted before assessing the risk posed by the species. For each species, species' common names, scientific names and synonyms were used to search for the literature and filter the search by the information provided in the abstracts and titles. In addition, we used terms like "invasive alien plants", "fleshy-fruited", "IAS", "introduced plant species", "non-indigenous plants", "ecological impacts", "economic impacts" and "negative impacts" to search for papers. All the references of the selected publication were screened and included as grey literature.

Impact assessments

Different impact assessment tools have been developed to quantify the impacts of invasive species (Nentwig et al. 2016; Nkuna et al. 2018). For this study, we used the Generic Impact Scoring System (GISS) as it integrates both ecological and socio-economic impacts (Nentwig et al. 2016) and has proven to be useful in assessing the impacts of invasive plants globally, including in South Africa (e.g. Novoa et al. 2016; Nkuna et al. 2018; Shivambu et al. 2020). The GISS is divided into two main categories, environmental and socio-economic impacts, each with six different mechanisms. The environmental impacts consist of impacts (1.1) on plants or vegetation, (1.2) on animals, (1.3) through competition, (1.4) through disease transmission, (1.5) through hybridisation and (1.6) on the ecosystem. The socio-economic include impacts on (2.1) agricultural production, (2.2) animal production, (2.3) forestry production, (2.4) human infrastructure (2.5) human health and (2.6) human social life. For each category, the impact level ranges from 0 (no known impacts or data deficiency) – 5 (highest impact) and the scenarios are described to ensure consistency (details on Nentwig et al. 2016). The overall impact scores (environmental and socio-economic) per species were used for analyses.

Traits of plants

Plant and fruit morphological traits influencing the invasion success of fleshy-fruited invasive alien plants are well documented. For each of the plant species, we compiled data that included mean fruit size, seed size, number of fruits and crop size (Suppl. material 1).

Data analyses

The differences between the overall and mean impact scores for each species' socio-economic and environmental impacts were tested using a paired t-test. We tested the differences between the mechanisms for environmental and socio-economic impact for each plant species using ANOVA. We used Kendall's rank correlation to test the correlation between the overall impact scores per plant and the number of papers used for each species. To explore the effects of plant species' functional traits with the environmental and socio-economic impact (sum of the six mechanisms), we fitted linear mixed-effects models. The functional trait data were log-transformed because of the non-normal distribution. We used the package lme4, libray nlme and function lme in R with the plant species traits as explanatory variables and the impacts as the response variable. To account for the phylogenetic relatedness, the species family was specified as a random effect (random ~ 1 | a). All the data were analysed using R statistical anlysis v.3.4.4 (R Core Team 2018).

Results

A total of 103 publications were used to score the impacts of 16 fleshy-fruited invasive plant species. There was no significant difference between the overall environmental and socio-economic impacts (Welch's t.test: P = 0.42). Amongst the 16 invasive plant species, lantana (*L. camara*) (impact magnitude = 42) and the tree of heaven (*A. altissima*) (impact magnitude = 32) had the highest cumulated impact scores (Table 1). Environmental impacts scores were higher for lantana and the camphor tree (*Cinnamomum camphora*) than the other species (Table 1). The highest socio-economic impact scores were recorded for lantana and tree of heaven (Fig. 1). Four plant species that had relatively little environmental impact presently included guava (*Psidium guajava*), inkberry (*Cestrum laevigatum*), the forget-me-not-tree (*Duranta erecta*) and the wax tree (*Rhus succedanea*). Two species that had no socio-economic impacts were coral bush (*Ardisia crenata*) and white mulberry (*Morus alba*). The tree of heaven scored the maximum impact on the socio-economic category through human social life (i.e. loss of recreational activities and tourist attractions, see Nentwig et al. 2016; Table 2). Some species showed low overall impact scores, but scored higher (the maximum impact score of five) in some mechanisms, for example, *M. alba* (impacts through hybridisation), *C. camphora* (impacts on plants or vegetation), *R. cuneifolius* (impacts on ecosystems) and *S. terebinthifolius* (impacts on plant or vegetation) (Fig. 1; Table 2). Most of the impacts recorded for the socio-economic category were through animal production, agricultural production and human health and the least impact was on human infrastructure (Fig. 2a; Table 2). There was a non-significant negative relationship between the environmental impact score and mean seed size and a significant relationship with mean fruit size (Fig. 3; Table 3). There was a non-

Table 1. The sum of environmental and socio-economic impacts scored for 16 fleshy-fruited invasive plant species using the Generic Impact Scoring System (GISS). Species that scored a maximum impact score of 5 in any of the mechanisms are highlighted in bold.

			GISS score			
Scientific names	Common names	NEMBA category	Environmental	Socio-economic	Total	Region of origin
Ailanthus altissima	**Tree of heaven**	**1b**	**13**	**19**	**32**	**Asia (China)**
Ardisia crenata	Coral bush	1b	3	0	3	Asia
Cestrum laevigatum	Inkberry	1b	0	3	3	South America (Brazil)
Cinnamomum camphor	**Camphor tree**	**1b**	**16**	**2**	**18**	**East Asia**
Duranta erecta	Forget-me-not-tree	3	0	1	1	America
Eugina uniflora	Surinam cherry	1a	2	2	4	South America (Brazil)
Lantana camara	Lantana	1b	23	19	42	Central and South America
Melia azedarach	Syringa	1b	3	2	5	Asia, Australia
Morus alba	**White mulberry**	**2**	**8**	**0**	**8**	**Asia**
Psidium guajava	Guava	2	0	6	6	America
Toxicodendron succedanea	Wax tree	1	0	3	3	Asia
Ricinus communis	Castor-oil plant	1b	4	2	6	Africa
Rubus cuneifolious	**American bramble**	**1b**	**10**	**4**	**14**	**North America**
Schinus terebinthifolius	**Brazilian pepper tree**	**1b**	**11**	**5**	**16**	**South America (Brazil)**
Solanum mauritianum	Bugweed	1b	12	7	19	South America
Syzgium jambos	Rose apple	3	5	6	11	South - East Asia

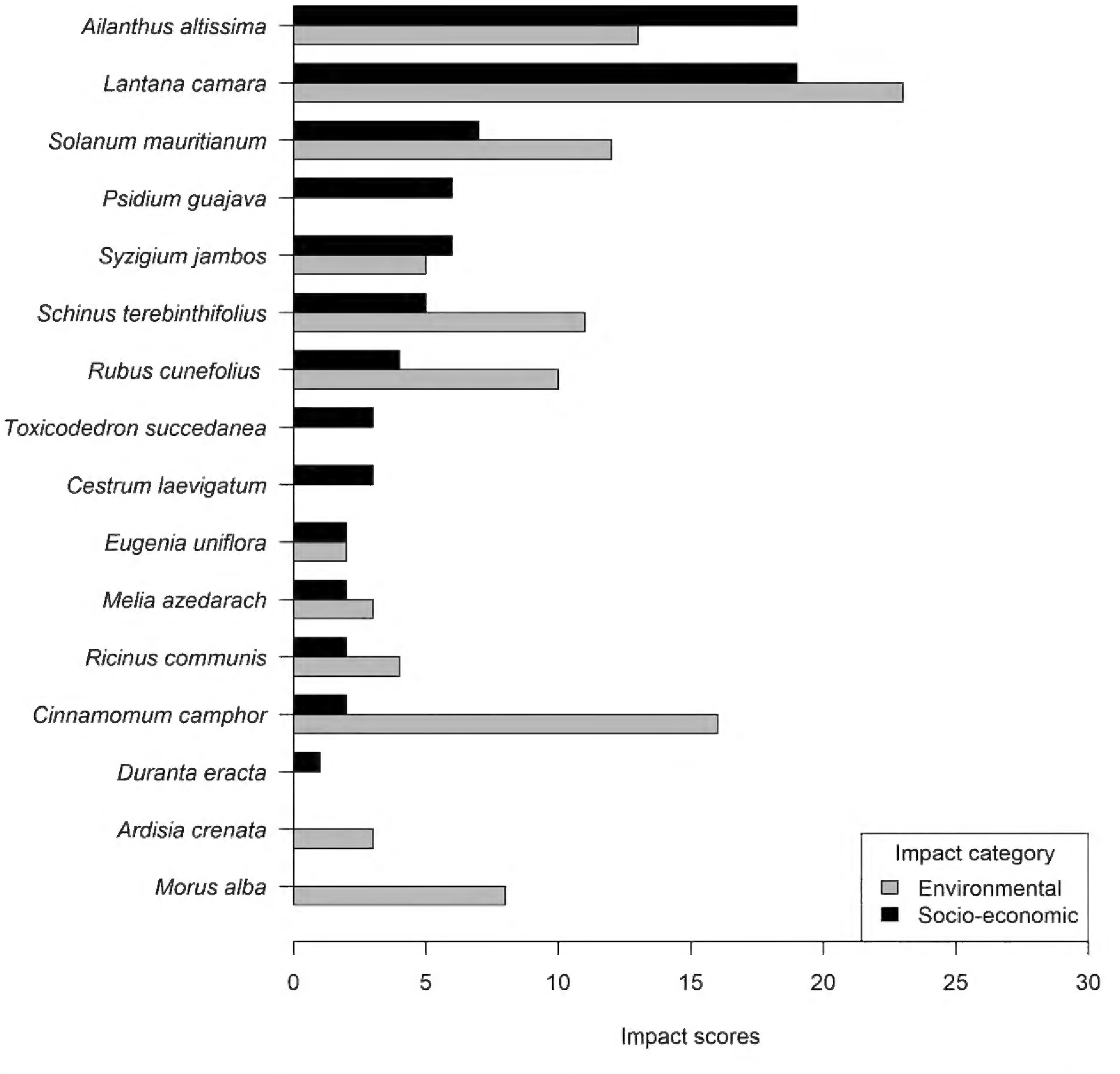

Figure 1. Impact scores for the socio-economic and environmental impact category for all the sixteen fleshy-fruited invasive plant species in South Africa in the present study.

Table 2. Environmental and socio-economic mechanism impact scores of fleshy-fruited invasive plant species assessed using the Generic Impact Score System (GISS).

Species	Common names	Environmental mechanisms							Socio-economic mechanisms								
		Plants or vegetation	Animals	Competition	Diseases transmission	Hybridization	Ecosystems	**Environmental total**	Agricultural production	Animal production	Forestry production	Human Infrastructure	Human health	Human social life	**Socio-economic total**	**Overall scores**	**Number of literature**
Ailanthus altissima	Tree of heaven	4	3	2	0	0	4	**13**	3	0	4	4	3	5	**19**	**32**	**17**
Ardisia crenata	Coral bush	3	0	0	0	0	0	**3**	0	0	0	0	0	0	**0**	**3**	**1**
Cestrum laevigatum	Inkberry	0	0	0	0	0	0	**0**	3	0	0	0	0	0	**3**	**3**	**5**
Cinnamomum camphor	Camphor tree	5	3	2	3	0	3	**16**	0	0	0	0	2	0	**2**	**18**	**1**
Duranta erecta	Forget-me-not-tree	0	0	0	0	0	0	**0**	0	0	0	0	1	0	**1**	**1**	**7**
Eugina uniflora	Surinam cherry	0	0	0	2	0	0	**2**	2	0	0	0	0	0	**2**	**4**	**1**
Lantana camara	Lantana	4	4	3	4	4	4	**23**	4	4	4	0	4	3	**19**	**42**	**25**
Melia azedarach	Syringa	0	0	0	0	0	3	**3**	0	0	0	0	2	0	**2**	**5**	**3**
Morus alba	White mulberry	0	0	0	3	5	0	**8**	0	0	0	0	0	0	**0**	**8**	**2**
Psidium guajava	Guava	0	0	0	0	0	0	**0**	3	0	3	0	0	0	**6**	**6**	**4**
Rhus succedanea	Wax tree	0	0	0	0	0	0	**0**	0	0	0	0	3	0	**3**	**3**	**2**
Ricinus communis	Castor-oil plant	3	1	0	0	0	0	**4**	0	0	0	0	0	2	**2**	**6**	**4**
Rubus cuneifolious	American bramble	3	0	2	0	0	5	**10**	0	2	2	0	0	0	**4**	**14**	**6**
Schinus terebinthifolius	Brazilian pepper tree	5	3	0	0	0	3	**11**	0	0	2	0	3	0	**5**	**16**	**10**
Solanum mauritianum	Bugweed	3	3	0	2	0	4	**12**	3	0	3	0	1	0	**7**	**19**	**8**
Syzgium jambos	Rose apple	0	0	2	3	0	0	**5**	3	0	3	0	0	0	**6**	**11**	**6**

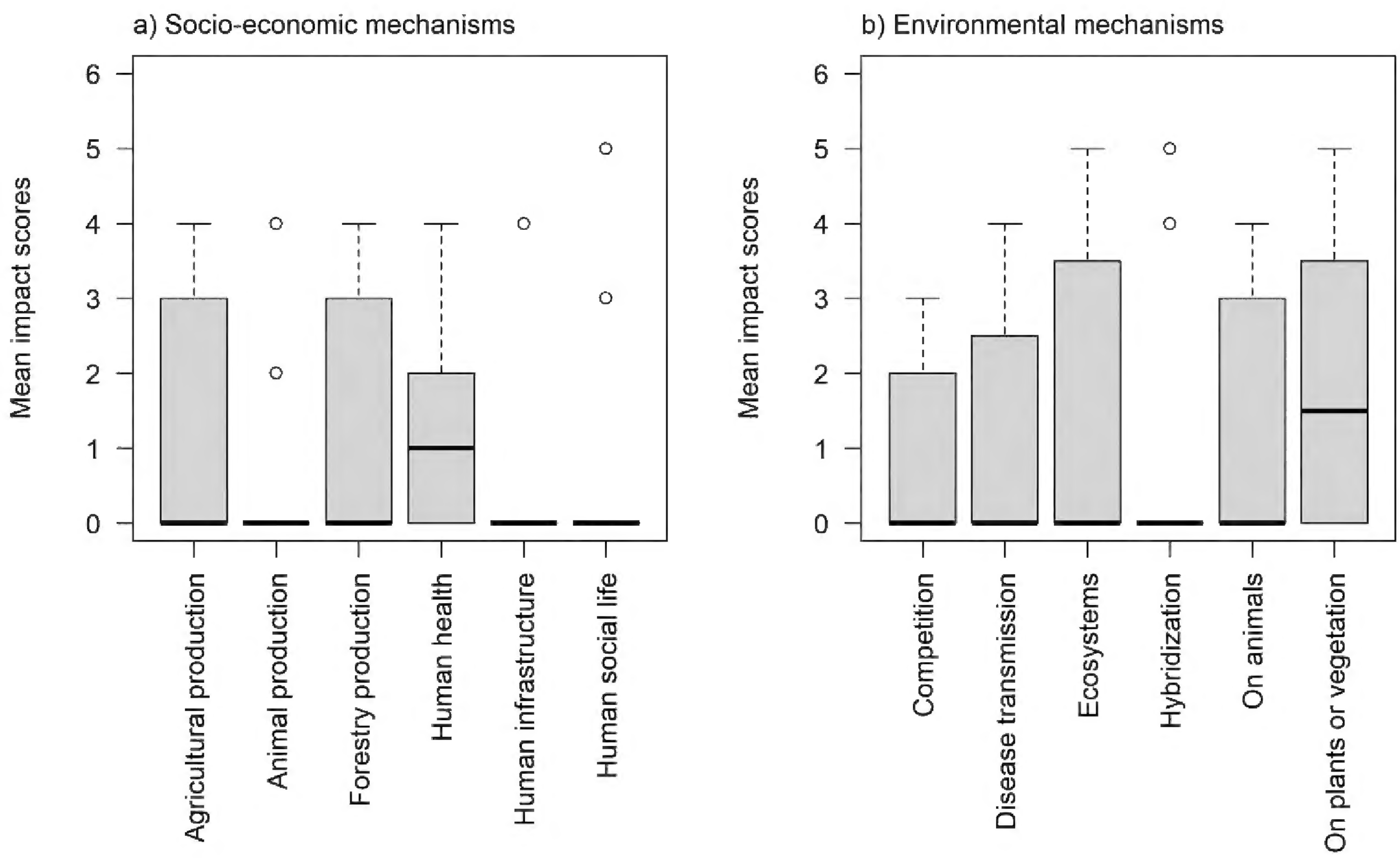

Figure 2. The mean impact scores for **a** the socio-economic mechanisms and **b** the environmental mechanisms in South Africa in the present study. (The boxes represent the mean impacts score in quantiles and the circles represent outliers).

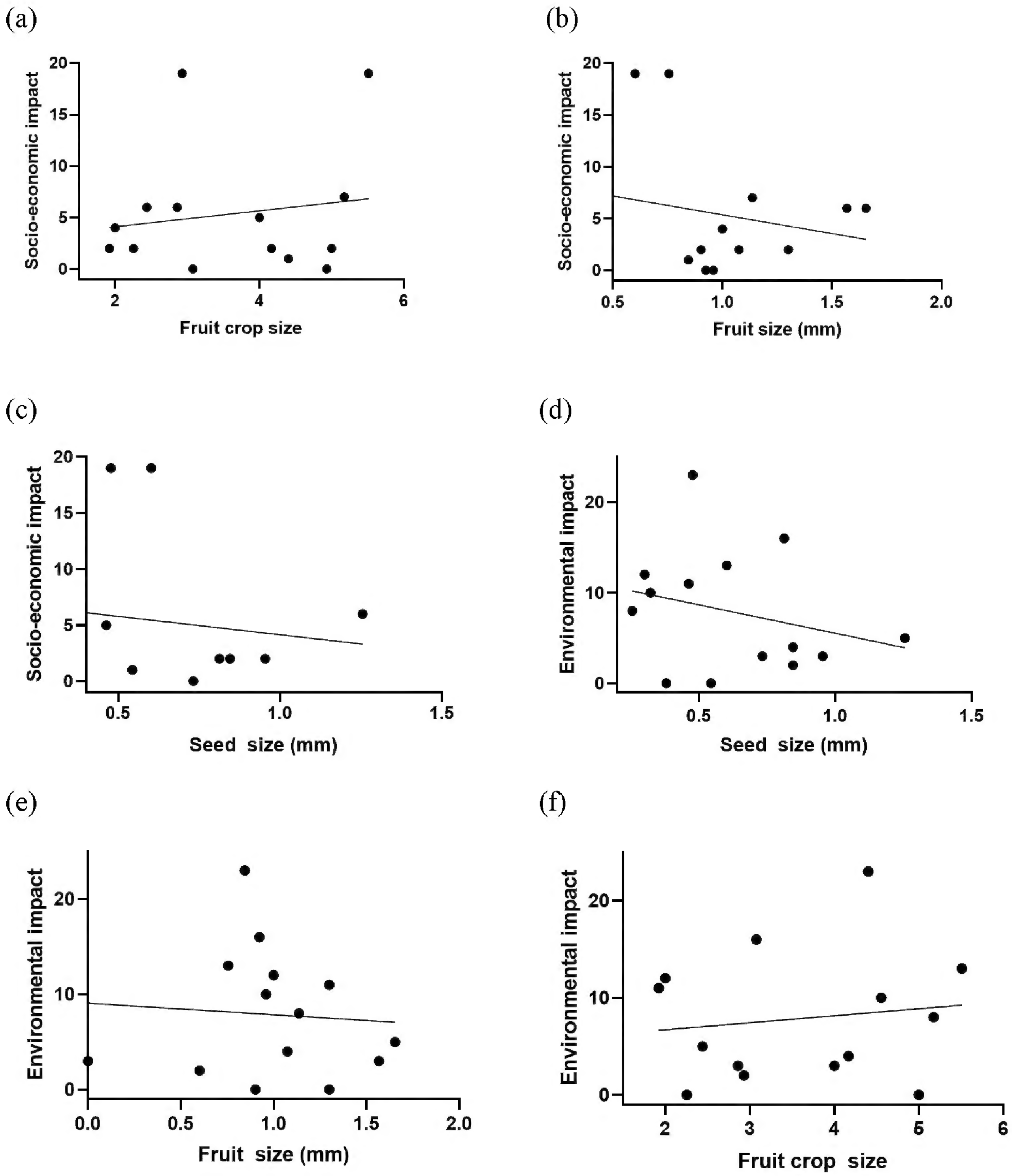

Figure 3. Relationship between socio-economic impacts with log-transformed morphological traits **a** mean fruit crop size **b** mean fruit size **c** mean seed size and environmental impacts with log-transformed morphological traits **d** mean seed size **e** mean fruit size and **f** mean fruit crop size. (Each dot represents a species).

significant positive relationship between socio-economic impact and crop size and a positive non-significant for mean seed size and mean fruit size (Fig. 3; Table 3).

Most environmental impacts were through impacts on plants or vegetation, ecosystem and animals and the least impacts were through hybridisation (Fig. 2b; Table 2). There were no significant differences in the impact magnitude of different mechanisms

Table 3. Linear mixed-effects model estimating the effect of fruit size, seed size and fruit crop size on the socio-economic and environmental impacts of avian dispersed alien invasive plant species in the current study. AIC is the Akaike Information Criterion.

Response	Model	Df	AICc	Log likelihood	P-value
Socio-economic impact					
	Log fruit size	12	93.17	-41.59	0.40
	Log seed size	12	92.91	-41.45	0.60
	Log fruit crop size	12	95.83	-42.92	0.59
Environmental impact					
	Log fruit size	12	91.72	-40.86	0.04*
	Log seed size	12	94.10	-42.05	0.34
	Log fruit crop size	12	96.71	-43.36	0.27

in both categories: socio-economic (ANOVA: df = 5, $P > 0.05$) and environmental (ANOVA: df = 5, $P > 0.05$, Fig. 2). We found that 14 (86%) of the 16 plant species had no records of causing socio-economic impacts through impacting human life and environmental impacts through hybridisation. Most records of alien invasive plant species were mainly for environmental rather than socio-economic mechanisms. The total number of papers used for the impact assessment was 103 (see Suppl. material 1 for a list of the data sources used) and there were significant differences between the number of papers and the scored impacts per plant (Kendall's Tau: $\tau = -0.15$; $p < 0.05$).

Discussion

In the present study, global impacts assessment of 16 fleshy-fruited invasive species indicated that 12 species had environmental impacts and 14 had socio-economic impacts. A total of six species in the present study showed either no environmental or socio-economic impacts. Similarly, a previous study in Europe that assessed the impacts of alien invasive plant species using the GISS showed no environmental or socio-economic impacts (Rumlerová et al. 2016). This is a consequence of studies focusing on certain impacts or the selection of species with already known impacts (Pyšek et al. 2012; Rumlerová et al. 2016; Schirmel et al. 2016; White et al. 2019). Previous studies have noted the influence of undocumented or lack of peer-reviewed information in quantitative impact assessment studies (McGeoch et al. 2012; Moshobane et al. 2019; Verbrugge et al. 2019). For example, *P. guajava* has major ecological impacts in Zululand, KwaZulu-Natal, South Africa, where this species has displaced native vegetation (C.T. Downs, unpublished data). Consequently, the impacts on the ecosystem or vegetation posed by this species are misrepresented in the present study. This highlights the importance of re-assessing the impacts of species once data are available or published in the case of using assessment tools that use peer-reviewed literature.

In the environmental category, we found impacts associated with fleshy-fruited invasive plant species were through the ecosystems, plants or vegetation impact mechanism and some species had the highest impact scores on these mechanisms,

for example, *R. cuneifolious*, *S. terebinthifolius* and *C. camphora*. These results correspond with previous studies showing similar findings on environmental impact mechanisms associated with invasive plant species (Vilà et al. 2011; Yazlik et al. 2018). For species with high scores, impacts on ecosystem functioning manifest in different ways, including integrating into ecosystem networks and changing seed dispersal and pollination networks which are important ecological processes. Through seed mutualism interaction, fleshy-fruited invasive plants alter the dispersal of other plant species and outcompete indigenous plants for dispersal agents (Mokotjomela et al. 2016). Consequently, changes in seed dispersal networks reduce overall biodiversity (Fuster et al. 2019) through the loss of ecological processes like pollination and seed dispersal. For example, in South Africa, *R. cuneifolius* alters pollination networks of native communities (Hansen et al. 2018) and disrupts bird-mediated ecological processes (Reynolds and Symes 2013). Some of the species with major impacts (i.e. *A. altissima*, *L. camara* and *S. terebinthifolius*) had impacts on vegetation and plants through allelopathy, negatively affecting native threatened plant species and overall biodiversity (Morgan and Overholt 2005; Sharma et al. 2005; Kowarik and Samuel 2007).

Impacts on human health, forestry and agricultural production were the main socio-economic impact mechanisms associated with fleshy-fruited invasive species in the present study, with *L. camara* and *A. altissima* having the highest impacts. Similarly, a study in Turkey showed that socio-economic impact mechanisms are through agriculture and human health (Yazlik et al. 2018). The major impact on forestry production may be because forests are identified as an important introduction pathway for many invasive tree and shrub species (Rejmánek 2014; Sitzia et al. 2016). Although some of these species are forest-edge species, they must be included in forest management (Sitzia et al. 2016). Impacts on agriculture and human health were indirect through hosting pests that damage agricultural crops or threaten human health. For example, *L. camara* harbours pests (e.g. tsetse fly *Glossina* spp.), resulting in major health issues in sub-Saharan Africa (Goulson and Derwent 2004). Additionally, alien fleshy-fruited plants form thick stands that generally reduce agricultural land's productivity and viability, resulting in reduced crop production of economically-important plants and increased management costs (Shackleton et al. 2017). It is important that the management of invasive plants is not only targeting protected areas and should be implemented in agricultural areas, as impacts associated with invasive plants are both environmental and socio-economic (Yazlik et al. 2018). This is particularly important for sub-Saharan African countries with agriculture-dominated economies, where livestock and crop farming constitute the largest agricultural sector (Pratt et al. 2017). Fleshy-fruited invasive species had relatively few or generally lower impacts on human infrastructure, except for *A. altissima*, which scored the maximum impact. This is mainly because the impacts of alien plant species on human infrastructure (e.g. roads, and traffic infrastructure, see Nentwig et al. 2016) remain poorly explored. Some species in the present study had low overall impact scores, but had the highest magnitude score for some mechanisms, for

example, *M. alba*, *C. camphora* and *R. cuneifolius*. In the United States of America (USA), *M. alba* has been reported to hybridise with an endangered native species *M. rubra* (Burgess et al. 2005), *C. camphora* replaces an endangered shrub *Ziziphus celata* in Florida, USA (Kaufman and Kaufman 2013) and *R. cuneifolius* threatens a grassland specialist plant in South Africa (Hansen et al. 2018). Similarly, a study that assessed the impacts of grasses using the GISS showed similar results where two grass species with low overall impact had high magnitude scores for certain mechanisms (Nkuna et al. 2018). This is particularly interesting as it raises an important question should species with high overall impact scores be considered as high priority or should species with low overall impact scores, but high magnitude scores for certain mechanisms, be of concern (Nkuna et al. 2018)? The overall impact scores can be useful in broad recommendations, but may negate the importance of specific species with specific impacts.

In the present study, there were significant differences between the scored impacts and the number of papers used; well-studied plant species scored significantly higher impacts than species with few or no impact studies. In general, the negative impacts of some species, especially those with economic value (i.e. *P. guajava*, *R. communis* and *R. cuneifolius*), are often overlooked because of their beneficial uses. The research efforts of assessing the impacts of economically-important invasive plants are potentially complicated by the trade-off between economic importance and their damage, resulting in misrepresentation of impacts. Indeed, Zengeya et al. (2017) assessed the impacts and benefits of invasive species and showed that the management of *P. guajava* has resulted in stakeholder conflict in South Africa because of the economic and intrinsic value of the plant. In addition, it has been reported that species with major economic impacts attract scientific attention, improving understanding of their ecological impacts (Pyšek and Richardson 2010). It was not the aim of this study to assess the limitations of this tool. Therefore, both scientists and decision-makers who aim to manage alien invasive species should consider both the benefits and costs of preventing the introduction of species with high impact scores or their management after introduction and establishment. This problem highlights the need for further studies to evaluate the socio-economic and ecological impacts posed by fleshy-fruited invasive plant species. Evaluating invasive species' social impacts will increase stakeholder engagement and scientific citizenship (Estévez et al. 2014; Crowley et al. 2017; Potgieter et al. 2019).

Species traits are important in the invasion success of alien plants (Pyšek and Richardson 2008). Our results of the impact relationship with morphological traits showed that species that produce large fruit crops of small fruit with small seed sizes have relatively higher environmental and socio-economic impacts. In cases where dispersal is limited to frugivores, fleshy-fruited plant species with large crop sizes are competitive, attract most species and are successful invaders (Ramaswami et al. 2017). For example, *S. mauritianum* has higher visitation rates than native and other plants alien to South Africa with relatively small crop sizes (Mokotjomela et al. 2013). Therefore, plant traits that influence seed dispersal interaction and invasion success are important and should

be incorporated into the screening process of fleshy-fruited alien plants (Jordaan and Downs 2012; Bitani et al. 2020). Species trait data of fleshy-fruited invasive species are comparable across different regions; therefore, the data can be transferable across regions (Jordaan et al. 2012).

Conclusions

Assessing socio-economic and environmental impacts of fleshy-fruited invasive plant species in South Africa showed that these species pose both ecological and socio-economic impacts. This study also highlighted that the impacts of many fleshy-fruited invasive species are not documented. We recommend management prioritise species with high overall impact scores (*L. camara*, *A. altissima* and *C. camphora*), including species with low overall impact scores, but high impact magnitude for certain mechanisms (*M. alba*, *R. cuneifoliu*, and *S. terebinthifolius*) as the impacts are inevitable. The introduction pathways of these fleshy-fruited invasive plant species need to be identified and managed to prevent their future spread. The present study results showed that different sectors are affected by invasive plant species, emphasising the need for the collaboration of stakeholders in biological invasion management. In South Africa, not all local municipalities have the capacity to effectively implement management strategies to manage invasive species (McLean et al. 2018). Therefore, despite the different mandates for different departments or sectors in South Africa, effective management of invasive plant species requires collaboration at a national and regional level, including and adding a socio-economic dimension to the management strategies to ensure inclusivity and transparency. This study is an important contribution in guiding managing invasive plant species and allocating limited resources in South Africa. We recommend that more research be done to evaluate the impacts, especially socio-economic impacts associated with fleshy-fruited invasive plant species.

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Supplementary material 1

Table S1

Authors: Nasiphi Bitani, Tinyiko C. Shivambu, Ndivhuwo Shivambu, Colleen T. Downs

Data type: Docx file.

Explanation note: The plant species' functional traits that influence seed dispersal by bird species as identified in Bitani et al. (2020).

Link: https://doi.org/10.3897/neobiota.74.83342.suppl1

Supplementary material 2

Table S2

Authors: Nasiphi Bitani, Tinyiko C. Shivambu, Ndivhuwo Shivambu, Colleen T. Downs

Data type: Docx file.

Explanation note: References used for the data summarised in Table 2.

Link: https://doi.org/10.3897/neobiota.74.83342.suppl2